

Fossil predation: did some clavilithine fasciolariid gastropods employ valve-wedging to feed on bivalves?

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ABSTRACT

Several gastropods, including members of the Busyconinae, wedge or chip bivalve prey by inserting the outer lip between the valves. This habit, which is associated with an abapically downwardly convex outer lip, often results in breakage and subsequent repair of the lip. I tested the hypothesis that convex-lipped clavilithines from the Eocene of France and the Neogene of Indonesia had higher frequencies of repair than their straight-lipped counterparts. Although this prediction was verified, frequencies of repair are low (0 to 0.19) compared to those of busyconines, indicating either that prey bivalves were small or that the predators are smaller than most busyconines.

INTRODUCTION

One of the most dramatic evolutionary transformations in the history of gastropods is the Cretaceous rise of predators (Taylor et al., 1980). Most of the diversification occurred in siphonate gastropods, especially tonnoideans, neogastropods, and related Cretaceous clades as discussed by Bandel & Dockery (2012). It has proven difficult to ascertain from shell morphology alone how these gastropods fed and what they ate. There are exceptions, however, and one of these is the subject of this paper.

Many neogastropods have a relatively thin outer lip whose edge is ventrally convex either throughout its length or anterior of its midpoint. In busyconine whelks and fasciolarine gastropods, this characteristic profile of the outer lip is associated with the ability of the gastropod to insert the shell lip between the valves of their bivalve prey (Kent, 1983a, b; Dietl, 2003a, b, 2004; Dietl et al., 2010; Durham et al., 2012). The same behaviour has been observed in Danish populations of the buccinid *Buccinum undatum* Linnaeus, 1758 (Nielsen, 1975), but other populations of this species do not wedge open bivalves (Scolding et al., 2007). In this connection it is interesting to note that some *B. undatum* have a convex lip whereas others do not. In thick-shelled species of the busyconine genera *Busycon* Röding, 1798 and *Sinistrofulgur* Hollister, 1958, the wedging behaviour has been modified into an edge-chipping

behaviour, in which the predator's convex lip sector is brought down forcefully at the valve commissure of thick-shelled prey (Carriker, 1951; Kent, 1983a, b; Dietl, 2003a, b, 2004). All these predators reach adult shell lengths of 60 mm or more, sometimes much more. Shell-wedgers tend to be limited to thin-shelled bivalve prey, whereas shell-chippers can open tightly closed thick-shelled bivalves as well (Paine, 1962).

Among possible fossil candidates for shell-wedging are members of a large group (probably clade) of Fasciolaridae that I shall refer to as clavilithines. After their earliest appearance in the Danian (Early Palaeocene) of Belgium as the small-bodied (37 mm) *Cosmolithes reticulatus* (Briart & Cornet, 1873) (see Glibert, 1973), the group achieved a worldwide cosmopolitan distribution during the Eocene. In the Early Oligocene, clavilithines persisted in Australia, the Gulf Coast region of the southeastern United States, southeast Asia and southern Europe. Miocene species are known from southern Europe, East Africa, southeast Asia and Australia. The last occurrence of undoubted clavilithines is in the Early Pleistocene of Indonesia. Whether the living *Cyrtulus serotinus* Hinds, 1843, which is endemic to the Marquesas Islands, also belongs here is uncertain (see below).

The genus- and species-level classification of the group remains contentious (Grabau, 1904; Weigley, 1927; Snyder, 1999; Beu & Marshall, 2011). At least 10 generic names have been proposed in the group (Snyder, 2003), but their characters and limits are ill-defined, and there is no current group-wide revision available. Following Beu & Marshall (2011), all species will here be referred to *Clavilithes* Swainson, 1840, in the broad sense.

Clavilithines have a characteristic shell form: a low to moderately high, often concave spire in which the whorls are spirally and axially sculptured; a more or less cylindrical, sometimes adapically keeled, adult whorl; a long, very narrow, straight siphonal protrusion; an elongate aperture whose non-reflected outer lip is either planar or abapically convex in ventral profile; the inner side of the outer lip smooth or (in *C. verbeeki* (Martin, 1895) and the living *Cyrtulus serotinus*) liriate; and a columella that is either smooth or bears an entrance fold to the siphonal canal. In many species there may be a second columellar fold. The inner lip of adult specimens in many species is raised and free, forming a thick ventral

shield in some large species. The posterior sector of the adult outer lip is often thickened and drawn out adapically.

Living shell-wedgers converge on the clavilithine morphology in having a long, straight siphonal protrusion and in having the non-reflected outer lip ventrally convex in its abapical sector. They differ from clavilithines in typically being larger, having a broader aperture and a wider siphonal canal, and in that the body whorl narrows abapically from its widest point, which is situated on its posterior third or half. Shell-wedging species today are sand-dwellers in shallow waters, a mode of life that was likely similar in clavilithines.

In shell-wedging and shell-chipping gastropods, predation attempts often result in slight breakage and subsequent repair of the convex sector of the outer lip. Individuals may show 10 or more such breaks in quick succession (Dietl & Alexander, 1998). If clavilithines with a convex lip engaged in similar predatory behaviour, comparable repaired breaks at the convex sector of the outer lip can be expected, and their frequency should be higher than that of breaks in clavilithines with a planar or straight lip. Here I test this prediction and place clavilithines in the wider context of the evolution of predatory gastropods.

MATERIALS AND METHODS

I examined collections of clavilithines at Naturalis in Leiden. Material came from the Eocene of France and the Miocene to Pleistocene of Indonesia. For each specimen, I measured shell length (or maximum diameter if the siphonal canal was broken) and noted the number of repaired scars on the last whorl. Each species was categorized as having either a planar or abapically convex outer lip. For each species, I pooled all samples to obtain a species-wide frequency of repair. If a sample from a single locality consisted of ten or more individuals, a sample-wide frequency of repair was calculated. Species identifications were based either on existing labels or on com-

parisons with identified specimens. For two samples, I was unable to determine the species-level taxon. *Clavilithes* sp. 1 from the Sables de Pierrefonde at St.-Gobain, France, has a smooth shell, abapically convex outer lip, erect inner lip, and a smooth columella without folds. *Clavilithes* sp. 2 also has a smooth shell, with a strikingly long, smooth siphonal protrusion, adherent inner lip, and adapically convex outer lip.

RESULTS AND DISCUSSION

Of the 10 species considered here, 3 have a near-planar outer lip and 7 have an outer lip whose anterior sector is convex (Table 1). The frequencies of repair are generally low, ranging from 0 in *C. deformis* (Solander in Brander, 1766) to 0.25 in *C. parisiensis* (Mayer-Eymar, 1876). In line with predictions, convex-lipped species have higher frequencies of repair (mean 0.15, range 0.05 to 0.25) than planar-lipped species (mean 0.04, range 0 to 0.10). The exact probability of obtaining rankings as extreme as or more extreme than that observed for the planar-lipped species is $4/120 = 0.033$ when the two taxa with a frequency of 0.10 are each assigned the rank of 5.

The difference in repair between planar and convex-lipped species cannot be accounted for by a difference in maximum size. The distribution of maximum size of planar-lipped species (ranked 2, 4, and 8) is indistinguishable from that of the convex-lipped species (ranked 1, 3, 5, 6, 7, 9 and 10).

At the scale of single localities, species often have frequencies of repair that are higher than the pooled frequencies (Table 2). Values are particularly high for *C. parisiensis* and *C. sp. 2* at Parnes (Middle Eocene) and for *C. verbeeki* at Odeng (Late Miocene).

It cannot be assumed that all repaired breaks result from unsuccessful attacks on bivalve prey. For example, the single break recorded for the planar-lipped *C. costarius* (Deshayes, 1834) affected the entire length of the lip and also resulted in

Age and Species of <i>Clavilithes</i>	Lip	Size (mm)	Frequency
Early Eocene			
<i>C. costarius</i> (Deshayes, 1834)	planar	35.8	1/31 = 0.032
<i>C. deformis</i> (Solander in Brander, 1766)	planar	62	0/15 = 0
<i>C. sp. 1</i>	convex	78	15/84 = 0.18
Middle Eocene			
<i>C. longaevus</i> (Solander in Brander, 1766)	convex	86	2/17 = 0.12
<i>C. noae</i> (Lamarck, 1803)	planar	98	6/58 = 0.10
<i>C. parisiensis</i> (Mayer-Eymar, 1876)	convex	100	14/56 = 0.25
<i>C. scalaris</i> (Lamarck, 1816)	convex	55	1/10 = 0.10
<i>C. sp. 2</i>	convex	82	5/29 = 0.17
<i>C. uniplicatus</i> (Lamarck, 1803)	convex	33	1/20 = 0.05
Late Miocene			
<i>C. verbeeki</i> (Martin, 1895)	convex	68	23/135 = 0.18

Table 1. Pooled species-wide frequencies of repair in clavilithines.

Locality and species	Frequency of repair
St.-Gobain	
<i>C. costarius</i>	1/27 = 0.037
<i>C. sp. 1</i>	15/84 = 0.18
Parnes	
<i>C. parisiensis</i>	8/22 = 0.36
<i>C. sp. 2</i>	3/11 = 0.27
Vaudancourt	
<i>C. parisiensis</i>	6/31 = 0.19
<i>C. noae</i>	3/37 = 0.083
<i>C. uniplicatus</i>	1/15 = 0.07
Palembang	
<i>C. verbeeki</i>	5/41 = 0.12
Angsana	
<i>C. verbeeki</i>	2/12 = 0.17
Odeng	
<i>C. verbeeki</i>	4/10 = 0.40
Kendeng	
<i>C. verbeeki</i>	4/25 = 0.16

Table 2. Sample-level frequencies of repair in species of *Clavilithes*.

the temporary loss of the siphonal protrusion. This kind of damage was probably caused by a predatory crab or other potential shell-breaker rather than by a prey bivalve. On the other hand, the repaired scars in *C. verbeeki* (Fig. 1) are more or less confined to the convex adapical sector, implying that the damage could have been inflicted by prey clams.

All frequencies reported here are low compared to those of Miocene to Recent shell-wedging or shell-chipping fasciolarines and busyconines. This implies that, if clavilithines did prey on bivalves, they did so on thin-shelled species whose valve adduction often did not damage the predators' shells. In this connection it must be noted that no clavilithines examined in this study exceed a length of 100 mm (Table 1), at the low end of the size distribution of living adult wedgers and chippers. Elsewhere, some clavilithines reach substantially greater sizes. I observed a specimen of *C. longaevus* (Solander in Brander, 1766) from the Sables d'Auvers at Ducy, France, with a length of 163 mm; and Vredenburg (1925) recorded a specimen attributable to *C. verbeeki* from the Mekran beds (Pliocene) of Pakistan with a length of 163 mm. Indonesian specimens of *C. fennemai* (Martin, 1906) from the Middle Miocene reach a length of 135 mm.

On the basis of shell morphology, it is unlikely that the living *Cyrtulus serotinus* wedges or chips bivalves. Its outer lip is strictly planar in profile and the aperture is quite narrow relative to that in other clavilithines, fasciolarines and busyconines. Grabau (1904) suggested that this species independently acquired its clavilithine character from a *Fusinus*-like ancestor; and although Wrigley (1927) was skeptical of this claim, Grabau may well be correct. Species of *Fusinus* Rafinesque, 1815 are likely vermivorous.

In the living fauna, shell-wedging and shell-chipping seem to be particularly prominent in warm-temperate and subtropical eastern North America. The few large tropical Indo-Pacific fasciolarines of the genera *Pleuroploca* P. Fischer, 1884 and *Filifusus* Snyder, Vermeij & Lyons, 2012 also prey on molluscs, and may use shell entry to do so, but there are no confirmatory observations of their predatory habits. With the



Fig. 1. *Clavilithes verbeeki* (Martin, 1895). RGM 8994, Indonesia, Java, Preanger Region, Odeng, Late Miocene, leg. R. Verbeek and M. Fennema. Note scar on last whorl indicated by arrows. Scale bar = 1 cm. Photo R. Helwerda.

Pleistocene extinction of clavilithines in the central Indo-West Pacific, however, the diversity and abundance of potential shell-wedgers must have declined substantially even as other predatory gastropods, including species with a labral tooth used for edge-drilling and valve penetration flourished (Vermeij, 2001).

Finally, many Cretaceous predatory gastropods also have a markedly convex lip. The possibility that they too were shell-wedgers should be investigated.

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REFERENCES

- BANDEL, K. & DOCKERY, D.T. III, 2012. Protoconch characters of Late Cretaceous Latrogastropoda (Neogastropoda and Neomesogastropoda) as an aid in the reconstruction of the phylogeny of the Neogastropoda. — *Freiberger Forschungshefte A* 542: 93-128.
- BEU, A.G. & MARSHALL, B.A., 2011. New Cenozoic records of genera and families from New Zealand (Mollusca, Gastropoda): highlights from Philip Maxwell's collection. — *New Zealand Journal of Geology and Geophysics* 54: 13-34.
- CARRIKER, M.R., 1951. Observations on the penetration of tightly closing bivalves by *Busycon* and other predators. — *Ecology* 32: 73-83.
- DIETL, G.P., 2003a. Coevolution of a marine gastropod predator and its dangerous bivalve prey. — *Biological Journal of the Linnean Society* 80: 409-436.
- DIETL, G.P., 2003b. Interaction strength between a predator and dangerous prey: *Sinistrofulgur* predation on *Mercenaria*. — *Journal of Experimental Marine Biology and Ecology* 229: 287-301.
- DIETL, G.P., 2004. Origins and circumstances of adaptive divergence in whelk feeding behavior. — *Palaeogeography, Palaeoclimatology, Palaeoecology* 208: 279-291.
- DIETL, G.P. & ALEXANDER, R.R., 1998. Shell repair frequencies in whelks and moon snails from Delaware and southern New Jersey. — *Malacologia* 39: 351-365.
- DIETL, G.P., DURHAM, S. & KELLEY, P.H., 2010. Shell repair as a reliable indicator of bivalve predation by shell-wedging gastropods in the fossil record. — *Palaeogeography, Palaeoclimatology, Palaeoecology*, 296: 174-184.
- DURHAM, S.R., DIETL, G.P. & VISAGGI, C.C., 2012. The mismeasure of behavior: natural history revision of prey preference in the banded tulip snail. — *Journal of Shellfish Research* 31: 101-109.
- GLIBERT, M., 1973. Révision des Gastropoda du Danien et du Montien de la Belgique I. Les Gastropoda du Calcaire de Mons. — *Mémoires de l'Institut Royal des Sciences Naturelles de Belgique* 173: 1-116.
- GRABAU, A.W., 1904. Phylogeny of *Fusus* and its allies. — *Smithsonian Miscellaneous Collections* 44: 1-157, 18 Pls.
- KENT, B.W., 1983a. Natural history observations on the busyconine whelks *Busycon contrarium* (Conrad) and *Busycotypus spiratum* (Lamarck). — *Journal of Molluscan Studies* 49: 37-42.
- KENT, B.W., 1983b. Patterns of coexistence in busyconine whelks. — *Journal of Experimental Marine Biology and Ecology* 66: 257-283.
- NIELSEN, C., 1975. Observations on *Buccinum undatum* L. attacking bivalves and on prey responses; with a short review on attack methods of other prosobranchs. — *Ophelia* 13: 87-108.
- PAINE, R.T., 1962. Ecological diversification in sympatric gastropods of the genus *Busycon*. — *Evolution* 16: 515-523.
- SCOLDING, J.W.S., RICHARDSON, C.A. & LUCKENBACH, M.J., 2007. Predation of cockles (*Cerastoderma edule*) by the whelk (*Buccinum undatum*) under laboratory conditions. — *Journal of Molluscan Studies* 73: 333-337.
- SNYDER, M.A., 1999. Notes on the molluscan genera *Clavilithes* Swainson, 1840 and *Rhopalithes* Grabau, 1904 (Gastropoda, Fascioliidae). — *Contributions to Tertiary and Quaternary Geology* 36: 3-8.
- SNYDER, M.A., 2003. Catalogue of the marine gastropod family Fascioliidae. — *Academy of Natural Sciences of Philadelphia Special Publication* 21: 1-431.
- TAYLOR, J.D., MORRIS, N.J., & TAYLOR, C.N., 1980. Food specialization and the evolution of predatory prosobranch gastropods. — *Palaeontology* 23: 375-409.
- VERMEIJ, G.J., 2001. Innovation and evolution at the edge: origins and fates of gastropods with a labral tooth. — *Biological Journal of the Linnean Society* 72: 461-508.
- VREDENBURG, E., 1925. Descriptions of Mollusca from the post-Eocene Tertiary formation of north-western India, Cephalopoda, Opisthobranchiata, Siphonostomata. — *Memoirs of the Geological Survey of India* 50: 1-350.
- WRIGLEY, A.G., 1927. Notes on English Eocene Mollusca, with descriptions of new species. II. Fusinidae. — *Proceedings of the Malacological Society of London* 17: 216-249.